number of words spoken and the number of "deviant" communications may have been counted or scored correctly, but replicate measurements on the same individuals under varying conditions of measurement could produce a variety of different regression weights, each of which might be used as a basis for the analysis of covariance. Perhaps in the case of determining the sex and age of subjects we can imagine procedures that would yield the same results across replications under practical circumstances, but the same cannot be said for most behavioral measurements.

The importance of these conditions for the analysis of covariance is as follows. If we represent the mean communication deviance score (the dependent measure) in the ith groups as $\bar{Y}_{i.}$ and the mean verbosity score (the covariate) as $\bar{X}_{i.}$, then the adjusted mean (θ_i) that is estimated and tested in the analysis of covariance is

$$\theta_{i.} = \bar{Y}_{i.} - b'\bar{X}_{i.}$$

where b' is the observed linear regression coefficient relating verbosity and deviance for this sample. The expected value of this expression $[E(\theta_i)]$ can be shown to equal

$$E(\theta_{i.}) = \alpha_{i.} + (\beta - \beta')\alpha_{i.}'$$

where $\alpha_{i.}$ is a population parameter representing the deviation of the ith group mean about the grand mean on the dependent measure independent of the covariate, β is the true population regression weight, β' is the expected value of the error attenuated regression weight, and $\alpha_{i.}'$ is the deviation of the ith group mean about the grand mean on the covariate for the population. Detailed derivations of the above expression can be found in Overall and Woodward (*7*) and in Cochran (*8*).

As can be seen, the bias term $(\beta - \beta')\alpha_{i.}'$ will vanish if the true regression weight is known (that is, $\beta - \beta' = 0$) or if there is random assignment to groups under conditions in which the deviation of the group means about the grand mean on the covariate is zero in the population (that is, if $\alpha_{i.}' = 0$). It also has been shown that the bias term will vanish when the assignment to groups is nonrandom but, rather, based entirely on the observed covariate score (*7*). Otherwise, the covariance adjustment does not remove all of the original bias but leaves a fraction $(\beta - \beta')/\beta$. This remaining bias can produce either an *overestimate* or an *underestimate* and will disturb tests of significance. In the Wynne and Singer and in the Hirsch and Leff studies the bias term in the analysis of covariance cannot be assumed to be zero since the true regression coefficient is not known, and/or since differences in the intact groups may have caused the observed group differences on the covariate. Thus, the analysis of covariance can lead to erroneous conclusions when applied in these studies, and it should not be employed even as a partial basis for deciding if the Hirsch and Leff study has confirmed the findings of Wynne and Singer.

The above problem is serious and has stimulated several attempts to devise corrections that will remove all of the bias when the analysis of covariance is applied under these circumstances (*9*). In principle, these corrections could have been employed here. However, prior to such correction, a strong logical case must be made for testing the communication deviance hypothesis by using the analysis of covariance to partial out verbosity as if it were a conceptually distinct source of behavioral differences among groups. Among the 41 categories of responses that were summed to form the communication deviance score are a number of specific categories that could be interpreted as "causes" of wordiness. Among them are "extraneous questions and remarks," "odd, tangential, inappropriate remarks," "wordplay," and "repetition of words or phrases" (*1*, table 1). To the extent that communication deviance causes wordiness, it would seem inappropriate to attempt to use differences in wordiness as an explanation for observed differences in communication deviance. In fact, just the reverse might be true for a number of the 41 categories that make up the total deviance score of Wynne and Singer.

Finally, we note that the analysis of covariance would be desirable here only if it were clear that the Wynne and Singer hypothesis requires that the proportion of deviant responses be greater among the parents of schizophrenics, which is analogous to the hypothesis tested by the analysis of covariance. It can be argued that the significant difference between groups in total number of deviant responses is, in fact, consistent with the Wynne and Singer hypothesis, even if it is mediated through verbosity of the parents (*1*, p. 24). As Wynne and Singer have stated, their interest is in repeated forms of communicating and relating that would contribute over the years to the formation of character and personality.

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5 April 1977

Social Communication in Canids: Evidence for the Evolution of a Stereotyped Mammalian Display

Abstract. *The variability in the duration and form of the canid play bow was studied in infant coyotes, wolves, wolf-dog hybrids, beagles, and adult free-ranging dogs. Both duration and form showed marked stereotypy. It appears that the role of this context-specific social signal in the communication of play intention has been fostered by selection for "morphological" stereotypy.*

Despite a history of considerable interest in animal social communication (*1–3*), few data are available on the "anatomy" or form of signals that are used. Indeed, one of the basic concepts of classical ethology, the "fixed" action pattern, rarely has been studied quantitatively (*4–7*). The form of visual displays has been studied quantitatively in invertebrates, lizards, and birds (*4–7*); however, there are very few data for mammalian displays (*8, 9*). In addition, little is known about the ontogeny of mammalian displays (*2, 8, 10*). Available evidence has demonstrated clearly that some social signals show phenotypic plasticity and that selection can shape various components (for example, duration, inter-act interval, form, sequence) of a signal or set of signals (*1–7, 11–13*). In cases in which it would be important to reduce ambiguity in the communicated message, selection could operate on signal structure (as with any other morphological structure) to reduce variability. Furthermore, it also is possible for certain signals to be restricted to specific contexts. Below I report the results of an analysis of a specific canid "play invitation" signal, the bow (*14, 15*), that shows marked stereotypy both in duration and form.

The bow is an easily recognized canid social display (Fig. 1). When performing this motor act, the animal crouches on its forelimbs and remains standing on its hind legs. The bow is infrequently observed outside the context of play (*15*). The bows of the following groups of animals were analyzed: 12 infant coyotes, *Canis latrans*; 4 infant wolves, *C. lupus*; 4 infant wolf-malamute hybrids; 13 infant beagles, *C. familiaris*; and 16 free-ranging domestic dogs over 1 year of age (age verified by owners). Infants were observed from about 20 to 90 days of age in a variety of situations. Some of the infants were hand-reared, and periods of social interaction with conspecific agemates were limited only to times when observers were present. For these infants, it was possible to record the first occurrence of the bow during social interaction. Other infants were mother-reared in seminatural conditions, and observations commenced when they emerged from the den that their mother had dug or from the den box that I provided. The free-ranging dogs were observed on the campus of Washington University (St. Louis, Missouri) and in and around Nederland, Colorado.

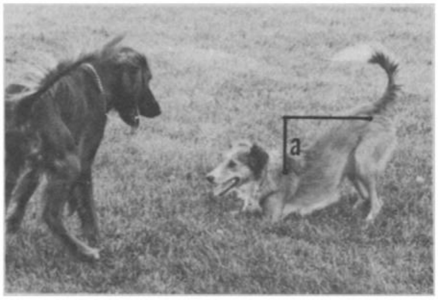

Fig. 1. A bow performed by the dog on the right. Form was measured on a grid system as the vertical displacement of the shoulders (*a*; see text). Lie of the hair around the shoulder was a reliable marker.

Animals were photographed with a super-8 or 16-mm movie camera (film speed, 64 frames per second). Films were analyzed with a single-frame analyzer. Camera speed was checked prior to each analysis to correct for possible error. Both duration and form were measured for bows that occurred in the beginning of a sequence (that is, the first act) and during a sequence. Duration was measured by counting the number of frames during which the individual remained crouched. The number of frames was then multiplied by 0.0156 second (= 1 frame) to convert to a measure of time. Means, standard deviations, and coefficients of variation were then calculated. Form was measured as declination of the shoulders relative to standing height on a grid system (Fig. 1, *a*). In order to standardize for individual differences in size as well as for changes in size with age, the height of the body at the shoulders was divided by 10, and a grid system of ten equal segments was used. Each grid unit was divided into fourths. Two observers independently took measures for each data point, and measurements were taken only when vertical displacement of the shoulders could be observed unambiguously. Interobserver agreement was consistently between 90 and 95 percent. For each group of animals, data from different rearing conditions were lumped because *no* significant differences were detected. In addition, data for the wolves and wolf-malamute hybrids were combined because the two groups were indistinguishable.

The mean duration of bows performed at the beginning of sequences for the infant coyotes, wolves (and hybrids), beagles, and adult free-ranging dogs was 0.31, 0.38, 0.33, and 0.32 second, respectively. Only the wolves differed significantly from the other groups ($F = 2.93$, d.f. = 3,436, $P < .05$). Mean duration of bows performed during play bouts was on the average 0.03 to 0.07 second shorter than mean duration of bows at the beginning of play sequences, and there were no significant differences between the groups, although the bows performed by the wolves were slightly longer. The longer duration of the wolf bows may simply be due to the greater body weight of young wolves when compared to coyotes and beagles of the same age (*16*). For coyotes, beagles, and adult dogs, bows performed during an interaction showed significantly higher variability in duration than bows performed at the beginning of sequences (Table 1). The greater variation in duration for bows performed during a sequence can be explained by the fact that these bows were preceded by a variety of different acts from which the individual went into the bow. On the other hand, the bows that occurred at the beginning of sequences almost always took place after the individual had been standing upright for a few seconds or as part of an approach.

Table 1. The variability, expressed as the coefficient of variation (%), of bows performed at the beginning of and during play bouts by three canid species. Form was measured on a grid system (see text and Fig. 1). The number on the left of the slash (/) refers to bows that were performed at the beginning of play bouts, and the number on the right of the slash refers to bows that were performed during an on-going interaction. The differences between the coefficients of variation for bows performed at the beginning of and during play bouts were tested for statistical significance by using the "c" statistic (*17*); see footnotes. The bows performed by the infant coyotes showed significantly less variability in form than those performed by the other groups. For example, when the bows of the coyotes were compared with those of the wolves, the differences were highly significant (for bows performed at the beginning of a bout, c = 3.46, d.f. = 169, $P < .001$; for bows performed during a bout, c = 3.04, d.f. = 119, $P < .01$). The significance of play signals for highly aggressive infant coyotes when compared with less aggressive infant wolves and beagles is discussed in (*15*) and (*23*).

Species	Number of bows	Coefficient of variation (%)	
		Duration of bows	Form of bows
Coyotes ($N = 12$)	73/57	9.68/13.79*	5.49/6.55†
Wolves + wolf-dog hybrids ($N = 8$)	98/64	10.53/11.43†	8.02/9.77†
Beagles ($N = 13$)	116/81	15.15/18.75‡	9.71/10.57†
Adult dogs ($N = 16$)	153/114	21.87/28.13§	10.87/12.70†

*c = 2.70, d.f. = 128, $P < .01$. †$P > .05$. ‡c = 2.20, d.f. = 195, $P < .05$. §c = 2.79, d.f. = 265, $P < .01$.

All groups showed significantly less variability ["c" statistic (*17*), $P < .02$] in form when compared to duration. Furthermore, there were no significant differences in form between bows performed at the beginning of and during sequences, although in all cases bows performed during sequences were slightly more variable.

In addition to there being a high degree of stereotypy, especially in the form of the bow, it is important to stress two other findings: (i) there were no significant changes in the variability of bows performed by infants of different ages (*18*), and (ii) the first bows performed by individuals who had been hand-reared (*19*), and who had not previously interacted with another individual or seen a bow, did not differ either from subsequent bows performed by that "isolate" or from the first observed bows performed by individuals who had been group-reared. The observed stereotypy when coupled to these observations (and also to the lack of differences between older animals reared in different conditions) provide evidence that there is a strong genetic component underlying this behavioral pattern.

The data presented herein are the first (to my knowledge) of their kind for a mammalian display. When compared to data on invertebrates and other vertebrates (*5–7, 13*), the bow is seen to be an equally stereotyped display, even for the adult free-ranging dogs. That is, the bow is a "relatively fixed" or "modal" action pattern (*4, 5*). Indeed, there have been no analyses of signal form that have resulted in coefficients of variation equal, or nearly equal, to zero, and the implication of absolute (invariant) morphological rigidity in the term "fixed action pattern" is misleading (*4–7*) and apparently was not intended when the term was coined (*20*).

It has been suggested that the most stereotyped motor coordinations are those that are important in locomotion and communication (*7, 13*). The bow is a locomotor intention movement which also has signal value. Many factors may select for stereotypy in signal form. Certainly, anatomical constraints may be operating (*9, 21*). In addition, if one analyzes the situations in which bows (and other play signals in other species) are used (*15, 22–24*), it is entirely plausible that the signal value of the bow was increased via selection for stereotypy. When animals engage in social play, actions from different contexts [for example, sexual, predatory, aggressive (*14, 15, 22–24*)] are used. If play signals, such as the bow, are important in communicating play intention [that is, announcing that "what follows is play" (*14, 15, 22–24*)] and overriding the "meaning" of an aggressive signal (*23*), for example, then one would expect the play signal to be different from other types of signals and to be stereotyped so as to reduce ambiguity in meaning. Furthermore, there can also be a reduction in the number of contexts in which a signal is used (*2, 12*). In many mammals, signals that appear to function in the communication of play intent (i) are observed almost solely in the context of play (*15, 22–24*), (ii) are different from other types of social signals (*22–24*), and (iii) *appear* to be highly stereotyped. With respect to the canid play bow, these three criteria apply fully. In addition, it has been demonstrated in coyotes and other infant canids that signals that are used to solicit social play do function to reduce the likelihood of play grading into aggression (*23, 25*). In these (and possibly other) animals, there has been selection for signals that serve to communicate play intention, signals that have a "tonic" (*26*) effect in that they serve to change the probability distribution of subsequent responses by the recipient of the signal (*23*).

An analysis of the variability of individual motor acts does not provide any information about the ways in which these behaviors, stereotyped or not, are linked together to form continuous chains of behavior. It is possible for selection to operate on individual motor acts as well as on the order in which they are performed (*27*), and it has been suggested that behavioral sequences can serve display functions (*28*). That is, a sequence may function as a composite signal. For the infant canids used in this study, play sequences were more variable than nonplay sequences (*6, 25*). Therefore, it is possible that there are two sets of signals that are used in play. The first would be a play signal itself and the second would be the sequencing of the acts. In this way, the play intention of an individual could be communicated initially, and then the "play mood" could be maintained either by repeating play soliciting signals or by using the ongoing sequence as a play signal. In canids, play signals occur either in the beginning of play sequences or are randomly distributed throughout (*23, 25*). The proposed signal value of variable canid play sequences may be one reason for the observation that canid play signals seem to be more important in the initial soliciting of social play and less so for the maintenance of the "play mood" (*23*).

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